In June or May sometime Batehelder sent me three young Screech Owls. I sent them up to Chocorua. They were grey and lovely but with awful tempers and harsh voices. Two were later returned to him, and again sent up to Crowlands. They had lost their good feeling toward the one left with me and abused him somewhat, shunned him always. At last, late in August I think it was, I found him dead and plucked in the cage. A week or two later I put the survivors into a barrel with a live mouse. Neither caught it. They quarreled and the next morning one of them was dead and partly plucked. The day following the other died. I clipped all of their wings and took out the one not returned to Batchelder several times. He drew birds if they saw him but he often made a stump of himself and evaded observation. They were fond of small birds, mice, fish, and so-so of liver.

THE RELATION OF GENERA TO FAUNAL AREAS.

BY SPENCER TROTTER, SWARTHMORE COLLEGE, PENNSYLVANIA.

The relative antiquity of a genus is probably indicated by the greater or less departure of its several species and their varietal forms from a common ancestral type. The degree of departure may be the resultant of two opposing factors — first, the influence of conditions favoring segregation, as the character of the vegetation and the variety of habitat within the breeding range, and, secondly, the opposing factor, that of the inherent quality of resistance in the common ancestral type against the disrupting influences of environment and of variational tendencies. It is in the breeding ground or faunal area that we must look for the conditions which produce these changes in epidermal tissue and those minor departures in voice and habits that we recognize as constituting distinctive specific and varietal differences within a genus. These influences are operative in the breeding area at the period of greatest plasticity of the organism, and variations from

the common type thus produced would tend to become more firmly set in the new form through geographical or habitat isolation in the breeding season. During an extended period of time this differentiation would tend toward an equilibrium as the inherited characters strike a balance with the environment. Time, and the segregating influence of wide geographical areas, with their opportunity for varied climatic and vegetation habitats, appear as the responsible causes of the phenomenon of species and of species distribution.

This is so well-worn a theme that I must ask your pardon for bringing it forward. It seems to me worth while, however, to recall these underlying principles. It is a habit of mind to regard a species as very definitely related to its range. It is much more definitely related to its habitat. By this I mean that a species is much more likely to extend its range than to alter its habitat. And further, I feel convinced that temperature per se does not effect the sexual tissues of a species so profoundly as to set barriers to its breeding area. Temperature, rainfall, soil conditions, and topography affect the character of vegetation and this is apparently the most direct and dominant factor in the distribution of species.

In a paper read before the Delaware Valley Ornithological Club and published in 'The Auk' for July, 1909 I have stated my belief that the present geographical groups of species which we recognize as faunas are more or less temporary phases in a general northward spread of species during post-glacial times, and that the true interpretation of faunas is not to be found in any single condition, such as temperature, but is related to the geological history of a land. In the present paper I wish to bring forward the thought that in this very advance or northward spread we have the conditions which have broken an original common type into several varietal and specific forms.

Let us take, for example, the genus *Hylocichla*, a group of woodland Thrushes quite similar to one another, presenting, one might say, a minimum of departure from an ideal type, both in adult sexual and juvenal phases of plumage. It seems quite possible that a generalized ancestral form common to all may have existed

¹ The Geological and Geographical Relations of the Land-Bird Fauna of North-Eastern America, pp. 221–233.

during the Middle Pleistocene in a more or less restricted area south of the glaciers, and that in spreading northward after the melting of the ice sheet, certain individuals reached farther to the north than others, establishing breeding grounds in comparatively high latitudes. This ancestral type was undoubtedly one of the many species that characterized the forest fauna of the Pleistocene and spread northward with the spread of this forest during what geologists term the Glacio-Lacustrine sub-stage. The instinct to return to this northerly nesting area at each succeeding spring would become a fixed habit through inheritance, and this group of individuals, removed by its position from the swamping effects of intercrossing, would tend to hold any variations that developed by segregation, the inherent quality of resistance against disruption determining the degree of change. The specific forms we recognize as Hylocichla alicia, H. ustulata, and H. guttata, with their several varieties, are thus the more closely related northerly-breeding species, the nesting grounds of which now overlap one another. though the Gray-cheeked Thrush has advanced beyond the limits of the other two, quite to the tree-line, while the Olive-backed Thrush has spread somewhat beyond the breeding range of the Hermit. In these two last species I have observed in Nova Scotia a marked difference in habitat. The Olive-backed Thrush was invariably found during the breeding season in the tall and heavy growth of coniferous woods, while the Hermit Thrush frequented. almost entirely, the lighter, scattered growth, being especially abundant in burned-over tracts and in sprout-lands of birch. limited areas their nesting sites did not coincide and this habitat difference may have been responsible in the fixing of their specific characteristics by segregation.

These remarks on the Genus Hylocichla apply mainly to the eastern phase of distribution. In the Cordilleran region and on the Pacific slope the varied conditions of mountain topography have more profoundly disturbed the several types which have broken up into a number of varietal forms. On the eastern side of the continent we find a variety of Hylocichla aliciæ—the Bicknell's Thrush—occupying quite isolated areas during the breeding season. Hylocichla fuscescens, the Veery, is of a more southerly breeding range than any of the foregoing species, while

the Wood Thrush, *H. mustelina*, has not advanced beyond the Transition Zone.

The Genus Dendroica of the Mniotiltidæ presents the antithesis of this close likeness of specific forms. We have here a group of thirty-four species that are widely different from one another in color pattern and with breeding ranges, in many cases, coterminous. or at least markedly overlapping. A geographical analysis of the genus shows that the species fall into two equal numerical groups. One group of seventeen well-defined forms has a strictly northern breeding range as compared with another group of seventeen species that is mainly extra-limital, breeding in the sub-tropical or the tropical domain, certain forms being confined to insular areas in the Caribbean. Four species of this second group have forms that breed in the North American region, namely D. astiva. D. auduboni, D. gracia, and D. vigorsi. Of the first group of seventeen strictly North American species only three are limited to the western side of the continent — D. nigrescens, D. townsendi, and D. occidentalis, the remaining fourteen being highly characteristic of the eastern fauna.

Taking into account the large numerical element in this genus and the great variety displayed by its forms, together with the fact that one half of the recognized species are still confined to the tropical or sub-tropical area, there seems some evidence for believing that this group of birds is of considerable antiquity and that its area of characterization was somewhere in the Middle American region of tropical environment, possibly at a time when the Tertiary land borders of the Gulf and Caribbean were much more extensive than at present and when certain of the now island masses were more closely connected with the main continental land. With the disappearance of glaciers from the northern region certain primitive types spread northward, and I think we may recognize the vanguard of this movement in such species as D. striata, D. castanea, D. palmarum, D. townsendi, D. magnolia, D. tigrina, D. astiva and D. coronata. All of these forms reach a high northern latitude in the breeding season and some like the Black-poll and Palm Warblers, the Myrtle and Magnolia Warblers have been lured far into the Northwest, indeed quite to the Sub-Arctic, by the great stretch of coniferous forest. The wide overlap observed in the

breeding area of these species would seem to indicate, as in the case of the Thrushes above cited, a slow movement of one species upon the heels of another, overtaking one another in their gradual spread, and it is probable that the initial movement was made up of a less number of forms than is represented by the existing species.

The distribution of color has considerable significance as an indication of descent. The almost universal presence of white blotches on the tail feathers among the species of *Dendroica* and the presence of wing bars must have been the fundamental color marks of the common ancestral type. And it seems to me, further, that certain primitive varieties of this common ancestor are indicated by the greater likeness among some of the existing species. The similarity of such species as *striata* and *castanea* in the autumnal phase of plumage, and the streaky, brownish young of *coronata*, *tigrina*, and *palmarum*; the head patch common to some forms, the throat patch common to others in the adult plumage, the rump spot and other markings, are very evident features of some community of descent.

All this, however, is not to the point or purpose of the present paper. What I wish to show here is that a genus like *Dendroica* possesses evidence in the large number of its specific and varietal forms and in their wide extra-limital distribution of a disruption of some tropical or sub-tropical ancestral type at a remote time compared with such a genus as *Hylocichla*. Geologically we might express this by saying that the primitive specific types of *Dendroica* were of late Tertiary origin, whilst the Hylocichline type was broken up into specific forms during the Pleistocene. Birds have their geological history as well as do mammals and other forms of life and as we have not been able so far to find their fossil remains we must look for traces of this history in the specific characters and in the facts of geographical distribution.

Professor Osborne has cited the case of a mammoth 1 in the stomach of which were found the remains of flowering plants and grasses belonging to species that are still growing in northern meadows. Conservative estimates as to the time when this animal lived would carry us back some twenty-five or thirty

Osborne — "The Age of Mammals," page 420.

thousand years. It is probable that many existing species of birds frequented these ancient meadows and the encroaching woodlands of birch, alder and conifer. If not the identical species then at least a very near and closely similar parent form that had split off from a still more remote parental stock.

I have taken the genus Hylocichla and the genus Dendroica as presenting very wide contrasts in the number of specific forms and in degree of likeness. Any genus of land birds that we will analyze must reveal some features that point to its history in connection with the origin and distribution of its several species and their varieties. If a genus stands for anything it must stand for this origin of its several species from a common ancestral type, near or remote. If the distribution of a genus means anything it means the history of its species in relation to changes through environment and the fixation of characters by segregation. Overlap or coterminous breeding range is the logical sequence of the spread of a species or variety into the territory of another, either after the one in advance has become fixed or in habitat differentiation if advancing at the same time. The Transition Zone Fauna is a wide expression of this overlap and is a clear indication of the advance of types toward the north. It is not, however, a permanent expression, nor is any faunal area permanent. Viewed in the immense lapse of time it is a momentary glimpse of an endless biograph. I am constantly interested in reading items in the pages of 'The Auk' that refer to some species of bird observed in a locality to the north of its general breeding range.

In conclusion let me sum up the somewhat rambling matter of this paper in the following brief statements:—

- (1) The genus means an ancestral type that has split up into its present component of species and their varieties under the influences of geographic and habitat environment.
- (2) The forms thus divided become fixed through segregation in the breeding area either through difference of habitat or by extension of range.
- (3) Each original type must have possessed, and its descendants probably still possess, a certain greater or less resistance to disruption. A genus represented by a single species, or at most by a very small number, would seem to indicate a high degree of resistance, even though spread over a widely varied territory.

- (4) The greater antiquity of one genus as compared with another would seem to be indicated by the larger number of its species and their wider variation from one another, but this might be offset by a greater resistance against disruption so that the genus represented by only one species might be, in reality, quite as ancient as the numerically high one. Furthermore we cannot know how many forms may have died out in any genus.
- (5) A genus is definitely related to a geographical range, while its several species are more definitely related to habitat conditions within the range, especially the breeding area.
- (6) A fauna is an expression of the temporary adjustment of any group of living beings to given conditions of environment. No single factor conditions its components or its boundaries. In the sum of its conditioning factors character of vegetation is probably the most important determining influence. Unquestionably the changes which man has wrought upon the face of the country by the clearing of forests and the development of agriculture has profoundly influenced the distribution of many species of birds.
- (7) All species tend to spread, as their ancestral types have spread, wherever suitable habitats are accessible to them. Search for food, especially at the breeding season, is the motive. Heredity has fixed the migratory impulse. The long daylight of the northern summer has probably had a determining influence in the northward spread of ancient generic types and of their descendant species.¹

¹ E. A. Schäfer, F. R. S. On the Incidence of Daylight as a Determining Factor in Bird Migration. Nature, Dec. 19th, 1907.